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Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds

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Abstract Conservation of biodiversity on forest landscapes dominated by plantations has become an increasingly important topic, and opportunities to maintain or enhance biodiversity within these forests need to be recognized and applied. Riparian buffers of mature forest retained along streams in managed forest landscapes offer an opportunity to enhance biodiversity across these landscapes. However, influence of buffer width and structure of adjacent plantations on habitat use by birds is not well understood. We modeled probability of occupancy, while accounting for variable detection probabilities, for 16 bird species of regional conservation importance in the Ouachita Mountains of Arkansas, USA. We examined occurrence of breeding birds in streamside management zone (SMZ) buffers embedded in three structural classes of pine plantation: young open-canopy, closed-canopy, and older thinned plantations. Our occupancy models included a positive association

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with SMZ width for nine bird species associated with mature forests. Models for three early successional species (prairie warbler [*Dendroica discolor*], white-eyed vireo [*Vireo griseus*], and northern bobwhite [*Colinus virginianus*]) included a negative association with SMZ width. Occupancy models for Acadian flycatcher (*Empidonax virescens*), summer tanager (*Piranga rubra*), pine warbler (*Dendroica pinus*), prairie warbler, and northern bobwhite also included structural condition of adjacent plantations, but most species did not appear affected by condition of surrounding plantations. We found diverse responses among species to width of retained SMZs and structure of adjacent plantations; some species apparently benefitted from SMZs >100 m wide, while others benefitted from narrow buffers. Furthermore, most species traditionally associated with mature forests were common in narrow SMZs, regardless of width. Thus, optimal width of SMZs relative to avian conservation depends on the species of greatest conservation interest.

Keywords Arkansas · Birds · Forest management · Intensive forestry · Pine plantations · SMZ · Streamside management zone

Introduction

An estimated 264 million ha of planted forests existed worldwide in 2010 (FAO 2006, 2010). Among planted forests, plantations are typically even-aged stands of a single crop species, which are intensively managed for production of wood products. Planted forests and plantation forestry have emerged as an important alternative to indigenous forest for production of wood products (Sedjo 1999, 2001; Carle and Holmgren 2008). These forests also provide an economic incentive for landowners to reforest following timber harvest and to retain lands in a forested condition (Miller et al. 2009).

Pine (*Pinus* spp.) plantations are the dominant planted forests in North America, South America, and Oceania, and comprise a large proportion of planted forests in Europe, Asia, and Africa (Carle and Holmgren 2008). Across these landscapes, conservation of biodiversity has become an increasingly important topic, and biodiversity is emphasized in sustainable forestry certification programs such as the Sustainable Forestry Initiative® (SFI) and the Forest Stewardship Council (FSC) (Carnus et al. 2006; Brockerhoff et al. 2008; Miller et al. 2009). Although intensively managed plantations of pine provide habitat for a wide diversity of species, including endangered species (e.g., Clout and Gaze 1984; Estades and Temple 1999; Humphrey et al. 2000; Brockerhoff et al. 2005; Pawson et al. 2008), economically viable options to conserve biodiversity within these intensively managed landscapes need to be recognized. For forest birds, species diversity may be lower (e.g., Driscoll 1977; Mitra and Sheldon 1993; Gjerde and Saetersdal 1997; Lindenmayer et al. 2003) or similar (e.g., Clout and Gaze 1984; Estades and Temple 1999; Turner et al. 2002) in plantations compared to native forests.

In landscapes subject to active forest management, including pine plantation management, riparian buffers or streamside management zones (SMZs) are typically remnants of unharvested native forest, often retained along perennial and intermittent streams. Streamside management zones present an opportunity to maintain biodiversity within plantation landscapes. In addition to their primary role of protecting water quality (e.g., Johnson and Jones 2000; Kiffney et al. 2003; Ward and Jackson 2004), these riparian buffers provide mature-forest habitat that may be limited in intensively managed landscapes and may provide travel corridors or refugia for species sensitive to overstory removal (e.g., Rudolph and Dickson 1990; Machtans et al. 1996; Ash 1997; Lindenmayer and Hobbs 2004; Shirley and Smith 2005; Perkins and Hunter 2006). Areas of remnant forest such as SMZs promote landscape heterogeneity, and many studies have highlighted the conservation value of maintaining remnant forests within plantations (e.g., Friend 1982; Lindenmayer et al. 2002; Fischer et al. 2006). Consequently, SMZs are implemented throughout North America; they are mandated on most federal lands in the U.S. and widely recommended in forestry best management practices on private lands (Knopf et al. 1988; Kinley and Newhouse 1997; Lee et al. 2004).

Previous studies of forested riparian buffers suggest wide buffers have greater species richness than narrow buffers and abundance of forest-interior birds increases as widths of buffers increase (Darveau et al. 1995; Hodges and Krementz 1996; Meiklejohn and Hughes 1999; Peak and Thompson 2006). Although several studies have examined effective widths of riparian buffers for birds, many of those studies examined forested buffers embedded in agricultural lands (e.g., Stauffer and Best 1980; Keller et al. 1993; Spackman and Hughes 1995; Peak and Thompson 2006). Island biogeography theory (MacArthur and Wilson 1967) is often referenced to explain species diversity and use of these habitat fragments. However, studies on forested riparian buffers in agriculture-dominated landscapes may not be applicable to SMZs embedded in plantations across forest-dominated landscapes (e.g., Opdam 1991; Kilgo et al. 1997), and care must be taken in comparing results among these studies. In forested landscapes, SMZs typically differ from the surrounding matrix in tree species, density, or age, whereas adjacent lands in agricultural landscapes may lack suitable habitat for forest-obligate birds. Consequently, type and quality of adjacent habitats likely influence results of studies examining riparian buffers, and buffers of remnant forest embedded in a plantation matrix may represent useable habitat patches that differ simply in quality from the surrounding matrix (e.g., Wiens 1994).

Studies of SMZs in forests generally have not considered structure of adjacent plantations, and most studies have examined buffers surrounded by young (<10 years old) plantations (Dickson et al. 1995; Thurmond et al. 1995; Kinley and Newhouse 1997; Hagar 1999; Meiklejohn and Hughes 1999; Pearson and Manuwal 2001; Conner et al. 2004; Shirley and Smith 2005). However, genetically improved conifers under commercial plantation management (e.g., thinned, pruned, fertilized) can grow quickly, and harvest ages of 25–35 years are common in the southeastern U.S. (Miller et al. 2009). Therefore, plantations remain in the early successional stage for a relatively short period (usually <9 years) and can rapidly progress through several structural conditions. Consequently, structure of adjacent plantations may have significant effects on breeding bird responses to SMZ width, but these data are lacking.

To determine responses of birds to SMZ width and structure of surrounding plantations, we examined effects of both SMZ width and adjacent plantation structure on breeding birds of conservation importance. We modeled probability of occupancy for birds while accounting for detectability bias within a landscape comprised largely of pine plantations.

Methods

Study area

We conducted our study in the Ouachita Mountains of Arkansas, USA. All study sites were within 40 km of the city of Hot Springs, in Garland, Montgomery, and Saline counties. The Ouachita Mountains range from central Arkansas into east-central Oklahoma and consist of east–west oriented ridges and mountains with narrow to broad valleys. Elevations in the region range from 100 to 900 m. Sampled streams occurred at elevations of 110–317 m and drained adjacent slopes with elevations up to 457 m. Climate in the region is characterized by hot, humid summers and mild winters (Skiles 1981). Average monthly precipitation ranged from 8.4 cm in August to 16.3 cm in May, and average annual precipitation was 139.9 cm (Laurent et al. 1989).

Study sites were on lands owned and managed by Weyerhaeuser Company where the predominant forests consisted of loblolly-pine (*P. taeda*) plantations. Study sites were on the edge, or just outside the natural range of loblolly pine (Baker and Langdon 1990). Typical management of plantations consisted of clearcut harvesting followed by site preparation and planting of pines. As plantations aged, silviculture included control of competing vegetation and commercial thinning and pruning at approximately 17 years of age. In accordance with best management practices, SMZs were retained for both water quality protection and biodiversity conservation, and were typically mature forest (generally >50 years old) that regenerated naturally after initial logging in the early 20th century. Tree species comprising forests in SMZs were mostly oaks (primarily *Quercus alba*, *Q. rubra*, *Q. velutina*, and *Q. stellata*), but also included hickories (mostly *Carya texana*, and *C. tomentosa*), shortleaf pine (*P. echinata*), and other hardwood species such as red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), and blackgum (*Nyssa sylvatica*) (Melchiors and Cicero 1987). Streamside management zones enclosed first- and second-order streams that were either perennial or intermittent. Average channel width of streams was 2.7 m ± 0.2 SE (range 0.7–8.7 m) and 68% of streams had fish present.

Study design

From 1989 to 1994, we sampled three different sets of study sites. We sampled Set 1 during 1989–1990, Set 2 during 1991–1992, and Set 3 during 1993–1994. Each set consisted of 18 SMZ/plantation combinations that were selected based on availability to represent six SMZ width classes: 0 m; 1–20 m (mean = 12 m, range 6–17 m); 21–40 m (mean = 30 m, range = 21–39 m); 41–60 m (mean = 52 m, range = 43–59 m), 61–100 m (mean = 75 m, range = 61–96 m), and >100 (mean = 161 m, range = 101–246 m). However, we were unable to locate an SMZ >100 m within a thinned plantation for Set 1 (1989–1990), which left 53 study sites for analyses.

We used only SMZs that were completely contained in one of three different structural classes of plantation (young open-canopy, closed-canopy, and thinned). For the three plantation classes, we selected stands based on structural characteristics rather than age because structure can vary within an age class due to site preparation, spacing of pine seedlings, seedling survival, intermediate silviculture, and site quality. Young open-canopy plantations averaged 6.7 years old (range 2–10 years since planting) and had open canopies that allowed substantial herbaceous and woody plant growth in the understory. Closed-canopy plantations averaged 15.1 years old (range 9–21 years since planting) and had completely closed overstory canopies, limited light reaching the forest floor, and sparse ground-level vegetation. Thinned plantations averaged 17.7 years old (range 11–22 years since planting), were thinned ≤4 years prior to sampling (mean = 2.3 years), had an open canopy structure, and had a variable amount of understory and midstory development depending on thinning density and time since thinning.

For SMZs <100 m wide, we centered one 80 m × 200 m belt transect in each site, parallel with the stream and along the long axis of the SMZ. Along the center of each transect, we surveyed all birds within the plot (40 m on each side of the SMZ center;

Conner and Dickson 1980). For SMZs >100 m wide, we surveyed two, side-by-side, 80 m × 200 m belt transects. Total area sampled differed between SMZs ≤100 m wide (1.6 ha sampled) and those >100 m wide (3.2 ha sampled). For sites where two transects were sampled, we used data from only one transect the first year and the remaining transect the second year for analysis.

Bird surveys

We conducted bird surveys from May to mid-June of each year, and all surveys were completed within 3 h of sunrise. Each study site within a set (17–18 sites) was surveyed twice by 6 observers on separate days for 2 years, which yielded 24 surveys for each site. Surveys consisted of observers walking the center transect and recording all birds seen or heard within the 80 m × 200 m sampling plot during a 30-min period. Because birds were only recorded at a distance of 40 m on either side of the center transect, vocal detectability was maximized (Schieck 1997). We did not count birds flying non-stop over transects. Each observer was trained prior to surveys and data from each observer was checked for consistency throughout the study.

Data analysis

Presence of a species (occupancy) and the ability to detect presence of that species (detection) both determine whether a species is recorded at a site. Detectability estimates use variation among multiple surveys to determine probabilities of detecting a species when it is actually present at a site, and detection modeling can incorporate covariates such as time or habitat attributes (MacKenzie and Bailey 2004). Occupancy reflects the probability of species presence based on spatial and temporal variation and attributes of the habitat (covariates). We evaluated probability of occupancy (Ψ) after first modeling probability of detecting a species (p) using the method described by MacKenzie et al. (2002). We used the software program PRESENCE (MacKenzie et al. 2006; http://www.mbr-pwrc.usgs.gov/software/presence.html) to compare a priori logistic regression models. We first modeled detection probabilities with occupancy held constant (Ψ [.], p[covariates]); we then modeled occupancy using the best set of covariates for detection (MacKenzie et al. 2006).

For each species, we modeled detectability in a two step process. We hypothesized that time within the breeding season when surveys were conducted may have affected detectability. Therefore, we first compared three different time patterns and included the most parsimonious time effect as an additional covariate in detectability modeling. We compared the following three patterns of time: (1) detection increased or decreased in a linear fashion during surveys (Time linear); (2) detectability increased or decreased in an exponential fashion (Time exp.); and (3) detectability increased to a high, then subsided (Time quadratic). We then modeled detectability for each species using the following covariates: (1) the best covariate for time of survey within the breeding season that was determined in the first step; (2) year of survey (Year) to account for differences in potential detection between years in a set; (3) width of SMZ (Width); and (4) structure of the adjacent plantation (Structure). We included Structure and Width as detectability covariates because differences in density of adjacent plantation and width of these relatively open SMZs (compared to plantations) may have affected visual and auditory detections of birds. We compared all possible combinations of Year, Structure, and Width for detectability. We determined the most parsimonious model among all candidate models based on the value of Akaike's Information Criterion modified for small samples (AIC_c; Burnham and Anderson 2002).

Using the best covariates for detectability, we then compared models for occupancy based on Width, Structure, or constant occupancy among areas (Ψ [.]). We did not include interactions because of limitations in our data ($n = 53$ areas; Peduzzi et al. 1996). For overall models of occupancy, we compared values of AIC_c to determine the most parsimonious models. When two or more models comprised the best set for occupancy, we used multimodel inference by averaging parameter estimates of models within 2.0 units of AIC_{min} (Burnham and Anderson 2002). For model averaging, we calculated weights (ω_i) from only those models within 2.0 units of AIC_{min}. We computed weighted unconditional standard errors for each parameter in parameter-averaged models (Burnham and Anderson, 2002). We examined goodness-of-fit ($\hat{c}$) of the global model, which included all parameters for detection and occupancy, to assess degree of overdispersion in our data (Burnham and Anderson 2002; MacKenzie and Bailey 2004). Values of $\hat{c}$ that deviated greatly from 1.0 were considered overdispersed ($>1.0 =$ underestimated variances), and values >4.0 generally indicated incorrect parameterization (Burnham and Anderson 2002). When models were overdispersed ($\hat{c} > 1.0$), we used the overdispersion factor to compare models based on $QAIC_c$ (Burnham and Anderson 2002). To reduce the influence of occupancy models with imprecise or erroneous estimates, we removed candidate models that contained parameters with unusually large standard errors (e.g., infinite; Gutzwiller and Barrow 2001).

We conducted analyses on 15 bird species of regional conservation importance in the western Gulf Coastal Plain and Ouachita Mountains, USA as classified by Partners in Flight (PIF), and on brown-headed cowbirds, which are an ecologically significant nest parasite (Table 1). Partners in Flight determines conservation priority values for each

Table 1 Common and scientific names, species abbreviations, and associated habitat for 16 bird species of regional conservation importance included in analysis of occupancy and detectability in riparian buffers embedded in pine plantations in the Ouachita Mountains of Arkansas, USA

Species	Abbreviation	Habitat association
Acadian flycatcher (*Empidonax virescens*)	ACFL	Mature forest
Brown-headed cowbird (*Molothrus ater*)	BHCO	Early successional
Eastern wood pewee (*Contopus virens*)	EAWP	Mature forest
Hooded warbler (*Wilsonia citrina*)	HOWA	Mature forest
Louisiana waterthrush (*Seiurus motacilla*)	LOWA	Mature forest
Northern bobwhite (*Colinus virginianus*)	NOBO	Early successional
Pileated woodpecker (*Dryocopus pileatus*)	PIWO	Mature forest
Pine warbler (*Dendroica pinus*)	PIWA	Mature forest
Prairie warbler (*Dendroica discolor*)	PRAW	Early successional
Summer tanager (*Piranga rubra*)	SUTA	Mature forest
Eastern tufted titmouse (*Baeolophus bicolor*)	ETTI	Mature forest
White-eyed vireo (*Vireo griseus*)	WEVI	Early successional
Wood thrush (*Hylocichla mustelina*)	WOTH	Mature forest
Worm-eating warbler (*Helmitheros vermivorus*)	WEWA	Mature forest
Yellow-billed cuckoo (*Coccyzus americanus*)	YBCU	Mature forest
Yellow-throated vireo (*Vireo flavifrons*)	YTVI	Mature forest

species based on biological vulnerability factors, which are evaluated for each species to produce global, continental, and regional assessments (Rich et al. 2004). We selected species with regional combined breeding scores (RSC-b) ≥ 13 (Panjabi et al. 2005). Occupancy estimates are not useful if a species is present in all sites. Consequently, probability of occupancy was too high (~ 1.0) to conduct analyses on the following PIF species of regional importance: black and white warbler (*Mniotilta varia*), blue-gray gnatcatcher (*Polioptila caerulea*), Carolina chickadee (*Poecile carolinensis*), Carolina wren (*Thryothorus ludovicianus*), and Kentucky warbler (*Oporornis formosus*). Conversely, probability of occupancy was too low (<0.10) to conduct analyses on brown-headed nuthatch (*Sitta pusilla*), northern flicker (*Colaptes auratus*), northern oriole (*Icterus galbula*), orchard oriole (*Icterus spurious*), and red-headed woodpecker (*Melanerpes erythrocephalus*). Although alternative methods of analysis might be feasible for these overly abundant and rare species, we believed conducting different types of analysis for each species would create results that were not directly comparable among species.

Results

The best models for detectability (p) for worm-eating warbler (WEWA) and wood thrush (WOTH) included no covariates (Table 2). The best models for detectability of brown-headed cowbird (BHCO) and Louisiana waterthrush (LOWA) included only Width, whereas the best models for detectability for eastern wood pewee (EAWP), northern bobwhite (NOBO), pine warbler (PIWA), prairie warbler (PRAW), white-eyed vireo (WEVI), and yellow-throated vireo (YTVI) included both Width and Structure. Among models of detectability that included Width, detectability of Acadian flycatcher (ACFL), eastern wood pewee (EAWP), eastern tufted titmouse (ETTI), LOWA, NOBO, PIWA, pileated woodpecker (PIWO), summer tanager (SUTA), and YTVI increased with increasing SMZ width. Detectability of BHCO, PRAW, and WEVI declined with increasing SMZ width. Detectability of six species was affected by Time (linear or exponential), with detectability of ACFL and yellow-billed cuckoo (YBCU) increasing during the sampling season and detectability of ETTI, hooded warbler (HOWA), PIWO, and SUTA decreasing. Models for only two species (HOWA and YBCU) included Year, and no models of detectability included Structure alone.

Models of occupancy (Ψ) for Acadian flycatcher (ACFL), summer tanager (SUTA), pine warbler (PIWA), prairie warbler (PRAW), and northern bobwhite (NOBO) included both Width and Structure in the best model set, and probability of occupancy increased in wider buffers for ACFL, SUTA, and PIWA (Fig. 1). For ACFL, SMZs surrounded by thinned plantation generally had higher probabilities of occupancy than SMZs surrounded by closed-canopy plantations (Table 3); however, confidence intervals for Structure included 0, indicating Structure had little explanatory power. For ACFL, probability of occupancy reached 1.0 in SMZs approximately 130 m wide (Fig. 1). Using an averaged model, PIWA increased in occupancy with increasing Width, but occupancy did not reach 1.0 in SMZs <200 m wide (Fig. 1). Furthermore, SMZs surrounded by closed-canopy plantations generally had higher probabilities of occupancy than SMZs surrounded by young open-canopy plantations, but neither Width nor Structure were significant in the model. Probability of occupancy for SUTA increased significantly with increasing Width and reached 1.0 at a width of approximately 60 m (Table 3; Fig. 1). Furthermore, our best model for SUTA suggested SMZs surrounded by thinned plantation generally had higher

Table 2 Model parameters included in best model sets for occupancy (Ψ) and detectability (p) for 16 species of birds, values of AIC or QAIC for each model, difference from the best model in each set (ΔAIC), weight of each model within a set (ω), and model fit (overdispersion factor $\hat{c}$) for the global model (all occupancy and detectability covariates included)

Species	Model	AIC/QAIC	ΔAIC	ω	Global $\hat{c}$
ACFL	Ψ(Width), p(Structure, Width, Time linear)	645.05	0.00	0.63	1.37
	Ψ(Structure, Width), p(Structure, Width, Time linear)	646.80	1.75	0.37	
BHCO	Ψ(.), p(Width)	153.32	0.00	0.72	6.44
	Ψ(Width), p(Width)	155.21	1.89	0.28	
EAWP	Ψ(.), p(Structure, Width)	146.59	0.00	0.55	4.17
	Ψ(Width), p(Structure, Width)	146.99	0.40	0.45	
ETTI	Ψ(Width), p(Year, Structure, Width, Time linear)	774.52	0.00	1.00	1.54
HOWA	Ψ(.), p(Year, Structure, Time exp.)	390.22	0.00	0.73	3.14
	Ψ(Width), p(Year, Structure, Time exp.)	392.19	1.97	0.27	
LOWA	Ψ(.), p(Width)	212.33	0.00	0.65	5.16
	Ψ(Width), p(Width)	213.58	1.25	0.35	
NOBO	Ψ(Structure, Width), p(Structure, Width)	451.98	0.00	1.00	0.31
PIWA	Ψ(.), p(Structure, Width)	611.09	0.00	0.35	1.65
	Ψ Width), p(Structure, Width)	611.44	0.35	0.29	
	Ψ(Structure, Width), p(Structure, Width)	612.41	1.32	0.18	
	Ψ(Structure), p(Structure, Width)	612.49	1.40	0.17	
PIWO	Ψ(.), p(Structure, Width, Time exp.)	372.44	0.00	0.72	0.10
	Ψ(Width), p(Structure, Width, Time exp.)	374.33	1.89	0.28	
PRWA	Ψ(.), p(Structure, Width)	413.62	0.00	0.32	2.52
	Ψ(Structure, Width), p(Structure, Width)	413.64	0.02	0.32	
	Ψ(Width), p(Structure, Width)	414.69	1.07	0.19	
	Ψ(age), p(Structure, Width)	414.85	1.23	0.17	
SUTA	Ψ(Structure, Width), p(Year, Structure, Width, Time exp.)	376.74	0.00	1.00	0.01
WEVI	Ψ(Width), p(Structure, Width)	1492.72	0.00	1.00	0.69
WEWA	Ψ(.), p(.)	38.70	0.00	0.73	17.04
	Ψ(Width), p(.)	40.69	1.99	0.27	
WOTH	Ψ(.), p(.)	13.53	0.00	0.72	51.72
	Ψ(Width), p(.)	15.44	1.91	0.28	
YBCU	Ψ(.), p(Year, Time linear)	124.77	0.00	0.70	6.19
	Ψ(Width), p(Year, Time linear)	126.48	1.71	0.30	
YTVI	Ψ(.), p(Structure, Width)	124.33	0.00	0.59	4.48
	Ψ(Width), p(Structure, Width)	125.08	0.75	0.41	

See Analysis section for description of model parameters and Table 1 for definitions of bird species abbreviations

probabilities of occupancy than SMZs surrounded by young open-canopy or closed-canopy plantations, but Structure was not significant in the model.

Probability of occupancy for prairie warblers (PRAW) and northern bobwhite (NOBO) decreased with increasing Width (Fig. 1). The averaged model for PRAW suggested a

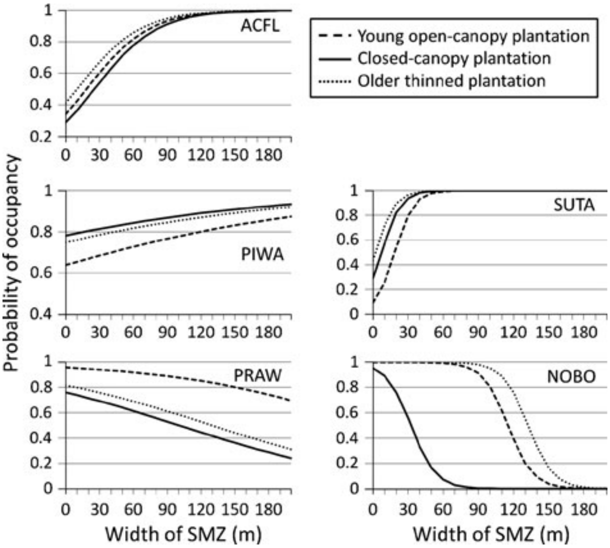

Fig. 1 Models for probability of occupancy for five species of birds where models included both effects of adjacent plantation structure and width (m) of streamside management zone. Occupancy was derived from 24 surveys of 1.6-ha plots centered on streams at 53 sites in the Ouachita Mountains, USA. Changes in occupancy based on width of buffer are given for each of the three plantation structural classes (young open-canopy plantations [open], closed-canopy plantations [closed], and older thinned plantations [thinned]). Species are Acadian flycatcher (ACFL), pine warbler (PIWA), summer tanager (SUTA), prairie warbler (PRAW), and northern bobwhite (NOBO)

non-significant decrease in occupancy with increasing Width, but less so in SMZs surrounded by young open-canopy plantations (Table 3; Fig. 1). Probability of occupancy for NOBO decreased significantly with increased Width; occupancy in SMZs surrounded by closed-canopy plantations reached zero in SMZs approximately 70 m wide, whereas occupancy in SMZs surrounded by thinned or young open-canopy plantations reached zero at ~170 m wide (Fig. 1).

Occupancy models for 11 species included Width, but did not include Structure, and models for seven of these species indicated increased occupancy with increasing Width (Fig. 2). For eastern wood pewee (EAWP), the averaged model indicated a non-significant change in probability of occupancy from ~0.9 in 0-m-wide SMZs to 1.0 in SMZs 40 m wide (Fig. 2). For yellow-throated vireo (YTVI), the averaged model indicated a non-significant increase in probability of occupancy from about 0.5 in 0-m-wide SMZs to 1.0 in 180-m-wide SMZs (Fig. 2; Table 3). For eastern tufted titmouse (ETTI), the averaged model for occupancy indicated occupancy increased significantly from 0.4 in 0-m-wide SMZs to 1.0 in 60-m-wide SMZs (Table 3; Fig. 2). Models of occupancy for Louisiana waterthrush (LOWA), yellow-billed cuckoo (YBCU), hooded warbler (HOWA), and pileated woodpecker (PIWO) suggested slight, but non-significant increases in occupancy with increased width of SMZ (Fig. 2; Table 3). For wood thrush (WOTH), fit of the global model was extremely poor ($\hat{c} = 51.72$), indicating a structural lack of fit and likely incorrect parameterization. Likewise for worm-eating warbler (WEWA), the global model had extremely poor fit ($\hat{c} = 17.04$). Therefore, we did not attempt to interpret results for WOTH or WEWA.

Models for two species that included only Width as an occupancy covariate decreased in occupancy with increasing Width (Fig. 2). The averaged model for brown-headed cowbird

Table 3 Parameter estimates for models estimating probability of occupancy for 16 species of breeding birds derived from 24 surveys of 1.6 ha plots centered on 53 streams in the Ouachita Mountains, USA

Species	Parameter	Estimate	SE	90% CI		Odds ratio
				Lower	Upper	
ACFL[a]	Intercept (open)	1.282	0.607	0.283	2.280	3.604
	Thinned	0.296	0.415	−0.387	0.979	1.344
	Closed	−0.255	0.380	−0.880	0.370	0.775
	Width	2.014	0.786	0.721	3.307	7.493
BHCO[a]	Intercept	1.015	0.348	0.443	1.587	2.759
	Width	−0.121	0.154	−0.374	0.132	0.886
EAWP[a]	Intercept	8.794	8.118	−4.560	22.148	6594.558
	Width	6.980	5.507	−2.079	16.039	1074.918
ETTI	Intercept	4.448	1.600	1.816	7.080	85.456
	Width	4.897	1.986	1.630	8.164	133.888
HOWA[a]	Intercept	0.933	0.306	0.430	1.436	2.542
	Width	0.028	0.089	−0.118	0.174	1.028
LOWA[a]	Intercept	1.337	0.373	0.723	1.951	3.808
	Width	0.318	0.285	−0.151	0.787	1.374
NOBO	Intercept (open)	5.716	3.511	−0.060	11.491	303.687
	Thinned	1.600	2.671	−2.794	5.994	4.953
	Closed	−7.701	4.183	−14.582	−0.820	0.001
	Width	−5.216	2.740	−9.723	−0.709	0.005
PIWA[a]	Intercept (open)	0.940	0.744	−0.284	2.164	2.560
	Thinned	0.516	0.434	−0.198	1.230	1.675
	Closed	0.702	0.655	−0.375	1.779	2.017
	Width	0.383	0.311	−0.129	0.895	1.467
PIWO	Intercept	0.847	0.549	−0.056	1.750	2.333
	Width	0.042	0.126	−0.165	0.249	1.043
PRAW[a]	Intercept (open)	2.504	1.791	−0.442	5.452	12.23
	Thinned	−1.631	1.225	−3.646	0.384	0.023
	Closed	−1.966	1.380	−4.236	0.304	0.140
	Width	−0.642	0.400	−1.300	0.016	0.526
SUTA	Intercept (open)	4.256	2.635	−0.079	8.591	70.527
	Thinned	2.001	1.809	−0.975	4.977	7.396
	Closed	1.358	1.763	−1.542	4.258	3.888
	Width	6.783	3.455	1.100	12.466	882.713
WEVI	Intercept	3.248	0.842	1.863	4.633	25.739
	Width	−1.526	0.567	−2.459	−0.593	0.217
YBCU[a]	Intercept	2.010	0.647	0.946	3.074	7.463
	Width	0.283	0.377	−0.337	0.903	1.327
YTVI[a]	Intercept	1.444	1.210	−0.546	3.434	4.237
	Width	1.532	1.254	−0.531	3.359	4.627

Models included effects of adjacent plantation structure (Open, Closed, or Thinned) and Width (m) of streamside management zone. Parameter estimates were based on either the best model or averaged model (when >1 model was included in the best model set). See Analysis section for description of parameters and Table 1 for definitions of bird species abbreviations

[a] Parameter estimates for these species were averaged from the best model set; SEs are weighted unconditional standard errors from averaged models

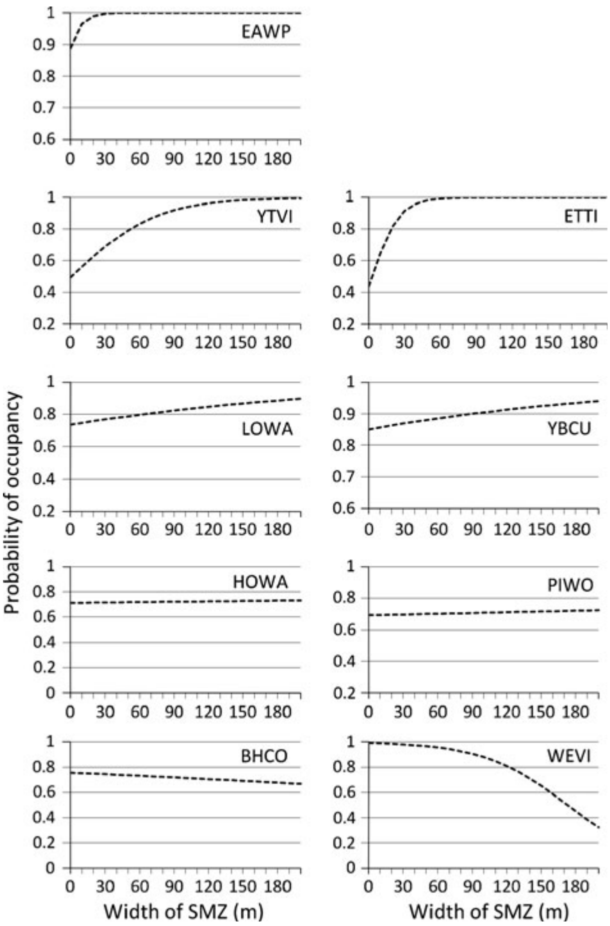

Fig. 2 Models for probability of occupancy for nine species of breeding birds where models included only effects of streamside management zone width (m). Occupancy was derived from 24 surveys of 1.6-ha plots centered on streams at 53 sites in the Ouachita Mountains, USA. Species are eastern wood pewee (EAWP), yellow-throated vireo (YTVI), eastern tufted titmouse (ETTI), Louisiana waterthrush (LOWA), yellow-billed cuckoo (YBCU), hooded warbler (HOWA), pileated woodpecker (PIWO), brown-headed cowbird (BHCO), and white-eyed vireo (WEVI)

(BHCO) occupancy indicated a slight, non-significant decrease in probability of occupancy with increasing Width (Table 3; Fig. 2). The best model for white-eyed vireo (WEVI) occupancy indicated a significant decrease in probability of occupancy from approximately 1.0 in SMZs <20 m wide to a probability of 0.3 in 200-m-wide SMZs (Table 3; Fig. 2).

Discussion

Streamside management zones in our study were relatively small patches of mature forest with abundant edge, which differed from adjacent pine plantations mostly in tree density, stand age, stand structure, and abundance of mature deciduous trees. Although SMZs provide benefits to many species, one benefit is providing patches of mature forest with abundant hardwoods in pine plantation-dominated landscapes for bird species that are mature-forest obligates. Aside from the ecological importance of riparian areas to moist-forest obligates such as hooded warbler, Acadian flycatcher, wood thrush, and Louisiana waterthrush (DeGraaf and Rappole 1995; Murray and Stauffer 1995; Smith 1977), effects of edge and size of forest patches (e.g., Moore and Hooper 1975; van Dorp and Opdam 1987) are both central issues in ecological responses of bird communities to forested riparian buffers. Increased rates of predation and nest parasitism by brown-headed cowbird (BHCO) are associated with edge and small blocks of forest such as narrow corridors (Robinson et al. 1995; Chalfoun et al. 2002; Thompson et al. 2002). However, studies suggest that parasitism rates by BHCO may depend more on landscape context, such as proportion of agricultural lands across the landscape, than on the distribution of temporary openings created by timber harvest (Robinson et al. 1995; Donovan et al. 2000; Howell et al. 2007). We found a slight, but non-significant decrease in occupancy of BHCO with increased width of SMZs, regardless of conditions of the surrounding plantation. Similarly, other studies suggest no significant effect of SMZ width on BHCO abundance in SMZs surrounded by young open-canopy plantations (Dickson et al. 1995; Conner et al. 2004). Consequently, width of SMZs embedded in plantations likely does not greatly affect presence of this detrimental nest parasite.

Studies suggest different minimum widths of riparian corridors are needed for mature-forest species, especially species that may be area-sensitive. Several authors have suggested that stream buffers ≥100 m are needed to maintain the complete avian community (Triquet et al. 1990; Hodges and Krementz 1996; Kilgo et al. 1998; Lambert and Hannon 2000), while others suggested widths ≥60 m are necessary to sustain most species (Darveau et al. 1995; Pearson and Manuwal 2001). However, these studies mostly examined buffers embedded in a single matrix type (typically recent clearcuts or agricultural lands), whereas our study examined both effects of buffer width and forest structure of the surrounding matrix. Our results suggest that patterns of bird occupancy associated with buffer width may be species-specific and dependent on the surrounding landscape, given that our model selection process included effects of adjacent plantation structure in 5 of 16 species.

Although not absent in narrow SMZs, we found species that are considered area-sensitive, interior-forest species that rely on mature forests (e.g., McIntyre 1995), including Acadian flycatcher (ACFL), Louisiana waterthrush (LOWA), pileated woodpecker (PIWO), pine warbler (PIWA), summer tanager (SUTA), eastern tufted titmouse (ETTI), yellow-billed cuckoo (YBCU), and yellow-throated vireo (YTVI) may benefit from wider SMZs. Conner et al. (2004) found abundance of ACFL, PIWO, YBCU, and YTVI increased substantially only in SMZs >60–70 m wide when surrounded by young, open-canopy forest. Among mature-forest species, our models suggested that probability of occupancy for ACFL and YTVI reached 1.0 in SMZs >100 m wide in the Ouachita Mountains. Other studies suggested abundance of ACFL is greatest in SMZs >60 m wide, whereas YTVI may benefit from SMZs >50 m wide when surrounded by young open-canopy plantation (e.g., Dickson et al. 1995; Conner et al. 2004). Nevertheless, we that found structure of adjacent plantations had little effect on occupancy of most mature-forest species.

Occupancy for other mature-forest species reached 1.0 at various SMZ widths. Occupancy of eastern tufted titmouse (ETTI) and summer tanager (SUTA) was greatest in SMZs ≥60 m wide. Although similar results have been found elsewhere for ETTI in SMZs embedded in young open-canopy plantations (Dickson et al. 1995; Conner et al. 2004), our results for SUTA suggest greater widths may be needed than those previously reported

(>30 m; Dickson et al. 1995). Although some studies suggest eastern wood pewee may not be affected by SMZ width (e.g., Conner et al. 2004), our model selection process included width of SMZ in the best model and suggested occupancy was greatest in widths >30 m.

Marczak et al. (2010) suggested that interior forest species are likely lost from riparian buffers with increasing time since buffer establishment and there is likely a time lag after initial buffer establishment and extirpation of interior-forest species. However, we did not find significant differences in occupancy for most interior-forest species (HOWA, LOWA, PIWO, YBCU, and YTVI) in SMZs surrounded by young open-canopy plantations (recently harvested) and older thinned plantations, suggesting occupancy of most interior, mature-forest species may remain stable throughout the rotation of adjacent plantations.

Our models for hooded warbler (HOWA), pileated woodpecker (PIWO), pine warbler (PIWA), and yellow-billed cuckoo (YBCU) suggested that SMZs >200 m may be required for probability of occupancy to reach 1.0. However, the lack of a strong relationship between SMZ width and occupancy for some species may have been more explanatory than the need for wide SMZs. For example, PIWO is characterized as an interior, mature-forest species that requires relatively large blocks of mature forest (McIntyre 1995). However, our association between SMZ width and occupancy of PIWO was weak and non-significant, suggesting unspecified model parameters may have had more influence on occupancy. Alternatively, presence of adjacent plantations may have mitigated effects of small patch size (e.g., Enoksson et al. 1995; Fischer and Lindenmayer 2006). The "continuum model" (Fischer and Lindenmayer 2006) suggests that suitable habitat may exist as a gradient in the matrix, allowing dispersal and survival in fragmented habitats. Consequently, functional size of a forest patch may be increased for area-sensitive species when it is surrounded by another type of forest (Harris 1984; Wilcove et al. 1986; Enoksson et al. 1995; Sargent et al. 1998). Adjacent plantations may provide habitat that compensates for preferred habitats or supplements resources over those found in preferred habitats (Norton et al. 2000; Brotons et al. 2005; Vallecillo et al. 2007).

Habitat characteristics that we did not include in analyses may have been more influential than width of SMZ or structure of adjacent plantations for some species. For example, pine warblers (PIWA) are greatly affected by presence of overstory pines and density of PIWA may be inversely related to deciduous vegetation within a stand (Conner et al. 1979). Because merchantable pines were sometimes harvested in narrower SMZs within our study area, wider SMZs may have had a greater density of mature pines than narrow SMZs. Therefore, our model for PIWA occupancy may have been biased by management that occasionally removed larger pines from narrow SMZs. In addition, hooded warblers (HOWA) are a shrub-nesting species that inhabit moist, mature forests in eastern North America (e.g., Thompson et al. 1992; Rich et al. 1994) and are strongly associated with dense understory vegetation (e.g., Robbins et al. 1989; Kilgo et al. 1996). However, we did not include abundance of understory shrubs in our analyses, which may have been less abundant in the interior of wider SMZs. Consequently, the presence of some species may have been more influenced by vegetation structure in some SMZs than by width.

Our models for prairie warbler (PRAW), northern bobwhite (NOBO), and worm-eating warbler (WEVI) indicated declines in occupancy with increasing SMZ width. Because we sampled a fixed area (1.6 ha) centered on each SMZ, we sampled portions of adjacent plantation habitats along narrow SMZs. Therefore, species associated with early-successional or shrubby habitats, including PRAW, NOBO, and WEVI (Hamel 1992; Annand and Thompson 1997; Larson et al. 2003; Rodewald and Vitz 2005) were more likely to be included in plots centered on narrow SMZs that sampled larger portions of adjacent shrubby habitats. We expected these three species to be abundant in narrow SMZs embedded in young open-canopy plantations or thinned plantations with abundant shrub layers. Thus, it is unclear if width of SMZ actually affected occupancy of these species within SMZs or they were simply counted in adjacent habitats more often in narrow SMZs.

We should note that five additional species of regional importance (black and white warbler, blue-gray gnatcatcher, Carolina chickadee, Carolina wren, and Kentucky warbler) were present in every SMZ, regardless of SMZ width or adjacent plantation structure, and were too abundant for occupancy analyses. Consequently, SMZ width may have had little effect on presences of these species. Further, abundance was too low to conduct analysis on five other regionally important species, including brown-headed nuthatch, northern oriole, orchard oriole, and red-headed woodpecker. However, these species are associated mostly with open woodland habitats (Hamel 1992), and we did not expect them to be abundant in densely forested riparian areas. We also caution that we measured only presence of birds in plots centered on SMZs and not productivity, and it is unknown how width of SMZs affected survival and reproduction of each species. These demographic parameters are crucial for assessing functional attributes of habitat patches.

Retained SMZs provide multiple functions in plantation landscapes that land managers should consider when deciding width, and optimal width of retained SMZs depends on forest management and conservation objectives. Conservation roles that may be considered include providing habitat for area-sensitive, mature-forest obligates in areas where that habitat is lacking, reducing fragmentation of early-successional habitat types, providing corridors for species such as salamanders that are sensitive to overstory removal, protecting water quality and aquatic communities, and protecting riparian-associated plants. To increase overall bird diversity across plantation-dominated landscapes, providing habitat for interior-forest species associated with riparian areas such as Acadian flycatcher may require some SMZs >100 m wide or retention of some larger riparian forest stands. Some studies suggest narrow buffers do not adequately maintain terrestrial fauna, especially interior-forest birds (e.g., Darveau et al. 1995; Hannon et al. 2002). However, narrow corridors do not necessarily create ecological traps for some mature-forest obligates (Chapa-Vargas and Robinson 2007). Because probability of occupancy did not reach zero in narrow SMZs for any species, narrow SMZs may provide some benefit, even for interior, mature-forest species. Other studies suggest patches of remnant forest $\leq$1 ha can have value as habitat for many vertebrates and invertebrates in plantations (e.g., Lindenmayer and Hobbs 2004; Davies and Margules 1998). Alternatively, other structural factors associated with individual SMZs, such as density of large pines or cover of understory shrubs could increase or diminish bird occupancy irrespective of SMZ width. In our study, SMZs were retained by the landowners in a variety of widths (including >100 m) to protect water quality and provide habitat diversity for wildlife. Collectively, these SMZs maintained most bird species of conservation concern expected to occur in upland riparian habitats in the Ouachita Mountains.

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